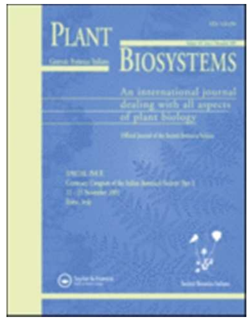
Structure, spatio-temporal dynamics and disturbance regime of the mixed beech–silver fir–Norway spruce old-growth forest of Biogradska Gora (Montenegro)

Published version:

DOI:10.1080/11263504.2014.945978

(Article begins on next page)



Structure, spatio-temporal dynamics and disturbance regime of the mixed beech-silver fir-Norway spruce old-growth forest of Biogradska Gora (Montenegro)

Journal:	*Plant Biosystems*
Manuscript ID:	TPLB-2013-0026.R2
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Motta, Renzo; University of Turin, Scienze agrarie, forestali e alimentari Bjelanovic, Ivan; University of Belgrade, Borgogno Mondino, Enrico; University of Turin, Curovic, Milic; University of Montenegro, Garbarino, Matteo; Univ. Politecnica delle Marche, Keren, Srdjan; University of Banja Luka, Meloni, Fabio; University of Turin, Berretti, Roberta; University of Turin, Nosenzo, Antonio; Univ of Turin, Dipartimento di Scienze agrarie, forestali e alimentari
Keywords:	old-growth forests, satellite images, forest structure, gaps, disturbances, coarse woody debris

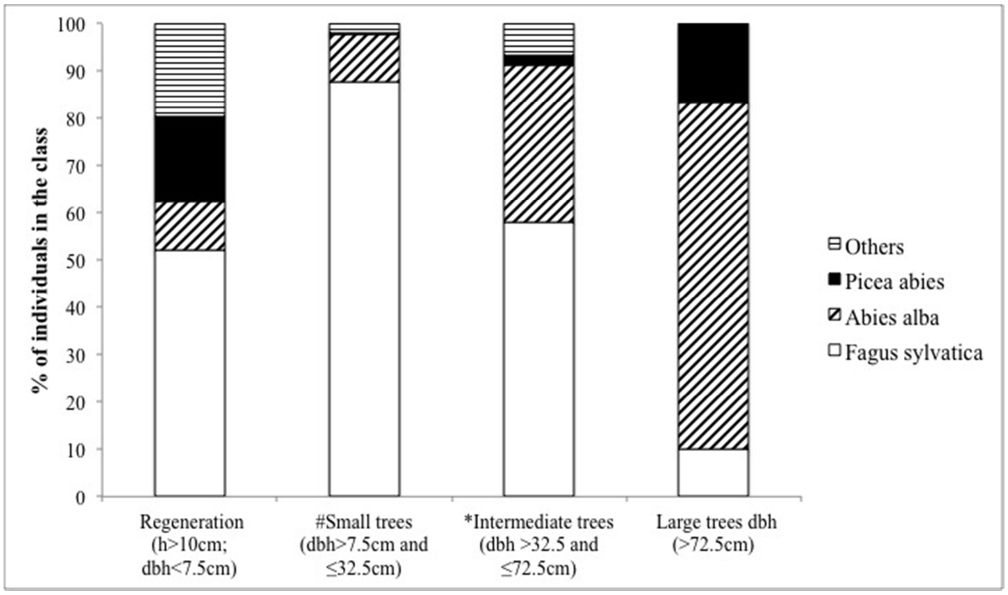


Fig. 4. Relative abundance of the most abundant tree species according to the size class (from regeneration to dominant trees) showing stratification of the species.

252x148mm (72 x 72 DPI)

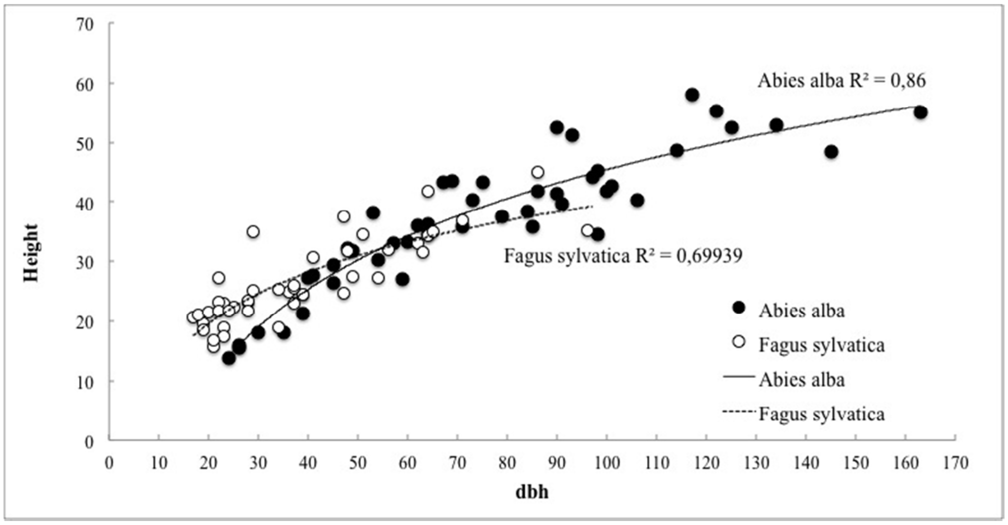


Fig. 5. Diameter-height relationships in beech and silver fir. The diameters are measured at the breast height (dbh)
276x142mm (72 x 72 DPI)

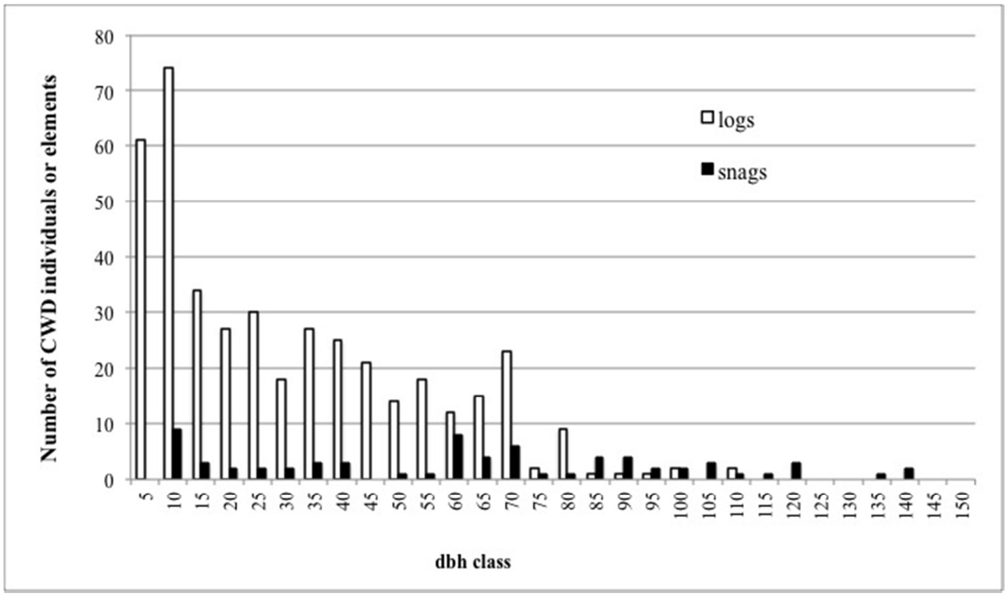


Fig. 6. Log and snag size distribution
253x149mm (72 x 72 DPI)

Running title: Biogradska Gora old-growth forest

CORRESPONDENCE: Renzo Motta, University of Turin, Department of Agriculture, Forestry and Food Sciences, Via Leonardo da Vinci 44, Grugliasco, Italy, renzo.motta@unito.it, +390116705538

Structure, spatio-temporal dynamics and disturbance regime of the mixed beech-silver fir-Norway spruce old-growth forest of Biogradska Gora (Montenegro).

Motta R.[1], Garbarino M. [2], Berretti R.[1], Bjelanovic I.[3], Borgogno Mondino E.[1], Čurović M.[4], , Keren S.[5], Meloni F.[1], Nosenzo, A. [1]

[1]University of Turin, Department of Agriculture, Forestry and Food Sciences, Via Leonardo da Vinci 44, Grugliasco, Italy

[2]Università Politecnica delle Marche, Department D3A, Via delle Brecce Bianche, I-60131, Ancona, Italy

[3]University of Belgrade - Faculty of Forestry, Kneza Viseslava 1, Belgrade, Serbia

[4]University of Montenegro, Biotechnical Faculty, Mihaila Lalica 1, Podgorica, Montenegro

[5]Faculty of Forestry, University of Banja Luka, Vojvode Step Stepanovica 75 a, Banja Luka, Bosnia and Herzegovina

Abstract

The structure and the spatio-temporal dynamics of the mixed beech-silver fir-Norway spruce old-growth forest of Biogradska Gora (Montenegro) have been analysed at different spatial scales: at the landscape scale, using a high resolution SPOT5 satellite image and at the stand level with an intensive field survey. This remote sensing approach has been used to obtain a land cover map in order to define the main vegetation types and to detect the large canopy gaps (> 150 m^2). The structural characteristics have been delineated in a 50 ha study area in which a regular 120 m grid was superimposed over a 1:10000 raster map and 30 sampling points have been obtained. The forest is characterized by a high volume of living trees (1029.6 m^3ha^{-1}) and coarse woody debris (420.4 m^3ha^{-1}) and by small-scale disturbances (individual trees to small groups) with a low incidence of intermediate disturbances (18 forest canopy gaps > 150 m^2 over 1230 ha). The two approaches have proved useful to delineate the spatio-temporal dynamics. The Biogradska Gora forest dynamics are dominated by very small-scale processes, which are partially autogenic and partially caused by allogenic factors. The influence of large scale or intermediate disturbances has shown to be negligible.

Keywords

Old-growth forest, satellite images, forest structure, gaps, disturbances, coarse-woody debris

Introduction

The structural analyses of forest ecosystems have shown that the temporal and spatial interplay between individual tree mortality and larger disturbances at varying scales, from small gaps to landscapes, creates a multitude of developmental pathways (Oliver & Larson 1996; Runkle 1982). The type and number of developmental stages may depend on different spatial scales, forest species and on the disturbance regime (Alessandrini et al. 2011; Franklin et al. 2002; Král et al. 2010) before the stage known as “old-growth stage” is reached (Franklin & Spies 1991). There are many definitions of this stage but most researchers agree that old-growth stands develops after long periods without any relevant human impact and major natural disturbances and show three main structural characteristics: old and large trees, abundant coarse woody debris in different decay stages and a multilayered vertical structure (Foster et al. 1996; Franklin 1993; Franklin & Van Pelt 2004; Motta 2002).

Characterizing the old-growth stage and the complete forest development cycle is particularly difficult in regions, like central-southern Europe, in which the anthropogenic effects have been of long duration and have interacted with natural factors so much that the effects of natural disturbance and human activities are now almost impossible to distinguish (Barbati et al. 2012; Garbarino et al. 2009; Motta et al. 2010). In this region human land-use has been the most important driving force behind the shaping of the landscape and the structure of the forest stands (Farrell et al. 2000; Garbarino et al. 2013). The forests have been intensively managed or cleared, and even in the most remote places there are signs of past grazing, litter collecting and charcoal production (Diaci et al. 2010; Gimmi et al. 2008).

The human impact has not been uniform over the entire region and substantial tracts of virtually untouched forests survived until the second part of the 19th century (Peterken 1996). In that period improvements in transportation and harvesting technology as well as the increasing demand for wood and fuel from industry have drastically reduced extent of the last remains of virgin forests. In the same time Forest administrations started to establish Forest reserves as hunting reserves or to preserve some parts of virgin forests (Diaci 1999). Most of these reserves were of relatively small, sometimes just a few hectares, while moderately sized and large reserves, from hundreds to several thousands of hectares, were extremely rare (Schuck & Hytönen 2000). Natural disturbances may operate at very different scales and the disturbance size could often be larger than the size of a small forest reserve. In order to accommodate these processes each forest reserve should be tailored to minimum size thresholds in order to allow all the disturbances the subsequent dynamic stages to develop. In small forest reserves effects can influence several factors and processes, such as the forest microclimate, tree mortality, animal habitat use, and the invasion of alien species (Gascon et al. 2000; Laurance et al. 2002). As a consequence most of the small reserves in central-southern Europe are not potentially able to capture the whole natural temporal and spatial variability (Cissel et al. 1999; Fraver et al. 2009; Landres et al. 1999) and large, well preserved forests are extremely important, from the scientific point of view, because of their potential role in the reconstruction of both the disturbance regime and the development stages of the forest with special reference to the old-growth stage (Burrascano et al. 2013; Marchetti et al. 2010; Ziaco et al. 2012).

One of the largest long-term preserved forests in central-southern Europe is in the "Biogradska Gora" National park (Montenegro). The history of measures adopted to protect this forest dates back to 1885 when, after the liberation of Kolašin from the Turks in 1878, the local people offered the Biogradska Gora forests to the duke (later the king of Montenegro) Nikola Petrović (Bilovitz et al. 2009). At that time most of the Bjelasica mountains forests were virgin or near-virgin forests that had never been significantly influenced by human activity (Peterken 1996). At the beginning, the forest was used as a royal hunting reserve, and in 1952 it was proclaimed a National park. In the core area of the park, the is the valleys of the Biogradska and Jezerštica rivers surrounding Biogradsko Lake, there are several different forest types, but the most important one is the mixed beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) type, with sparse Norway spruce (*Picea abies* (L.) Karst.) (Andjelić et al. 2012; Čurović et al. 2011a; Čurović et al. 2011b). The other relevant forest species that are present are: sycamore maple (*Acer pseudoplatanus* L. and *Acer platanoides* L.), mountain ash (*Fraxinus excelsior* L.), rowan (*Sorbus aucuparia* L.) and wych elm (*Ulmus montana* With.).

The main purpose of this study was to analyse the structure and dynamics of the beech, silver fir and Norway spruce mixed Biogradska Gora old-growth forest using both remote sensing and intensive ground control in order to: 1) describe its main structural characteristics, 2) reconstruct the spatio-temporal disturbance dynamics and 3) compare the structure and dynamics of this forest with other central-southern European mixed old-growth forests.

Material and methods

a) Study site

This research was conducted in the Biogradska Gora National park in the north-western part of the Bjelasica mountain range in the Dinaric Alps (Montenegro). This forest is the largest of a network of remaining virgin forest of the same forest type that can be found in the Balkans peninsula from Slovenia to Montenegro (Anić & Mikac 2008; Diaci et al. 2010; Maunaga 2001; Motta et al. 2011; Nagel & Svoboda 2008).

The lowest part of the park is in the Tara valley (about 830 a.s.l.) while the highest part is the Crna Glava peak (2139 m a.s.l.). The park covers an area of 5650 ha (Fig. 1). Different forest categories exist within the park but the most important ones are a) pure beech and b) mixed beech, silver fir and Norway spruce. The annual average precipitation at Biogradsko lake (1093 m a.s.l.) is 1962 mm, with a maximum in November and a minimum in July. The mean annual temperature is around 5 °C. The bedrock is mainly made up of eruptive rocks (Čurović 2011). Two forest types were identified in the mixed silver fir, beech and spruce forest on the basis of phytosociological relevés:: *Abieti-Fagetum dinaricum Treg. 1957,* and *Piceeto-Abieti-Fagetum s. lat*. Treg. 1957, the main difference between these being the occurrence of Norway spruce. According to the profiles and to the physical and chemical characteristics of soils they can be classified as brown acid – dystric cambisol (Čurović 2011).

b) Remote sensing

Owing the absence of forest maps a satellite image was used to analyse the vegetational cover and to identify the best site for the intensive study area. The study area for the remote sensing analysis comprised the core areas of the Biogradska Gora forest reserve (5883 ha). A high-resolution SPOT5 satellite image, acquired on May 14th 2007, was used. The acquired image was of the A1 type, and it included the panchromatic band (480-710 nm) with a 2.5 m GSD (Ground Sample Distance); three multispectral bands (Green, 500-590 nm; Red, 610-680 nm; Near Infrared, 780-890 nm) with a 10 m GSD and one Short-wavelength infrared (1580-1750 nm) with an original 20 m GSD, but supplied already resampled up to 10 m. The SPOT5 multispectral data were initially calibrated as reflectance at-the-ground values using the Gain and Offset values, as reported in the metadata file of the images. Atmospheric effects were taken into account and minimized using the Dark Subtraction algorithm (simplified approach) available in the ENVI 4.7 software (ITT 2009). The satellite image was orthoprojected using the rigorous Toutin model for SPOT5 data implemented in the Orthoengine module of the PCI Geomatics software. Thirteen 3D ground control points (GCPs) surveyed by a LEICA GPS System 1200 (GX 1230 receiver), were used in this process. The GPS double frequency measurements were post-processed using the Sarajevo permanent station which is part of the EUREF network (Bruyninx et al. 2012). The resulting planimetric accuracy was suitable for a 1:10000 scale map (1.3 m at BGO). The Digital Elevation Model used for the orthoprojection was the free available NASA/METI ASTER Global Terrain Model, which has a geometric resolution of 30 m and a vertical Root Mean Squared Error (RMSE) of about 9 m. Both the panchromatic and the multispectral bands were orthoprojected and a RMSE for the GCPs of 1.54 m was obtained. As the ground survey was mainly planned and performed to obtain a traditional forest structure characterization and not aimed at gathering information concerning the prevalent forest classes from a remote sensing point of view, the resulting data were considered not to be statistically or spatially suitable for the definition of the robust region of interest for use in a supervised classification.

Furthermore ground survey data were used to interpret and preliminarily validate the result of an unsupervised pixel-based classification. The classified images were the SPOT5 multispectral ones (GSD = 10 m) and the ISODATA algorithm was adopted using the following settings: number of classes = 5 to 10; Pixel % for convergence = 2%; max class STD = 0.25; Minimum Class Distance = 0.5; Minimum Number of pixels in each class = 100. This operation was performed in ENVI 4.7 and a land cover map composed by five categories after 32 iterations was obtained. On the basis of the ground data the clusters were interpreted as conifers, broadleaves, open/grassland, water bodies and unvegetated areas. The satellite images were also used for canopy gap detection (canopy gaps, sensu Runkle 1982, larger than 150 m^2). For this task an on-screen photointerpretation was performed (Garbarino et al. 2012)

c) Forest structure

The forest structure survey area (50 ha) was located in a north-eastern slope (centered at 42.53’13 N and 19.36’33 E) at an elevation ranging from 1210 to 1443 m a.s.l. A regular 120 m grid was superimposed to the 1:10000 raster map and 30 sampling points were thus obtained (Fig. 2). Four types of measurements were applied at each sampling point (Motta et al. 2011): (a1) the species and diameter at breast height (dbh, about 130 cm) to the nearest 0.01 m for all the living trees (dbh ≥ 7.5 cm) was recorded in a 615.5 m^2 circular plot (radius = 14 m); (a2) the species and height of each regeneration or suppressed individual (h > 10 cm and dbh < 7.5 cm) was recorded in a 113.1 m^2 round plot (radius = 6 m); (a3) the diameter of each log (diameter > 5 cm) crossing a 50 m line intersect oriented northward from the center of the sampling point (Van Wagner 1968), was measured (Motta et al. 2006) and (a4) the stumps (diameter at the ground and diameter at the top for diameter at the ground > 5 cm) and the snags/standing dead trees (dbh and height of the top for dbh>7,5 cm) in a 50 x 4 m rectangular plot centered on the previous line were also measured. For each element of CWD (logs, snags, standing dead trees and stumps) species (when possible) and decay class (Nagel & Svoboda 2008) were recorded (class 1 fresh, class 5 very old). Four-five tree heights, covering different species and diameter classes, were measured at each sampling point. The shape of each diameter distribution was determined by examining the significance and the sign of the model parameters (Alessandrini et al. 2011; Janowiak et al. 2008). The volume of the living and standing dead trees was calculated on the basis of local forest management volume tables. The volume of the logs, stumps and snags was calculated using methods that have been described in Motta et. al., 2006. Owing to the protection status of the forest it was not possible to core any of the living trees in order to reconstruct the age structure and to detect the releases. The maximum age for the dominant Norway spruce, silver fir and beech trees was estimated counting the tree rings on the stumps of recently broken off dominant trees.

Results

a) Forest cover and gaps

Most of the Biogradska valley is covered by forest (65.5%). Mixed conifer and broadleaf stands (*Abieti-Fagetum dinaricum* and *Piceeto-Abieti-Fagetum*), which are the subject of this study, cover 1230 ha at an altitude ranging from 1200 to 1500 m a.s.l. Pure broadleaf stands were detected at lower and at the uppermost elevations while pure conifer stands were observed in the montane and subalpine belts (Fig. 2). The remaining land cover types were unvegetated areas (21.5%) and grasslands (12.5%). A total of 53 openings, 18 forest canopy gaps sensu Runkle (1982) and 35 openings due to the geomorphological processes (e.g. landslides, rocks) or other processes unrelated to the forest dynamics, were found in the mixed *Abies-Picea-Fagus* forest and within the 1200-1500 m a.s.l. altitudinal belt,. The average size of the forest canopy gaps was about 985 m^2 and the median size was 672 m^2. A high gap size variability was observed ranging from 169 to 3025 m^2.

b) Forest structure

The density of the live canopy trees was 412 ha^{-1} (Tab. 1). The volume of living trees was 1029.6 m^3ha^{-1} and the basal area was 60.1 m^2ha^{-1}. The density of regeneration was 3102 individuals ha^{-1}. The diameter distribution (Fig. 3) exhibited a rotated sigmoidal form ($P < 0.05$) which is typical of old-growth stands (Alessandrini et al. 2011; Janowiak et al. 2008).

All the sampled plots had a multilayered vertical structure but the species distribution was not homogeneous over the different size classes. Beech was rather dominant among the regeneration, small and intermediate trees (Fig. 4). Silver fir, instead, was dominant in the large trees. The diameter-height relationships in the two most represented species, that are beech and silver fir, showed that the beech height is higher in smaller diameters compared to silver fir but an opposite relationship can be observed for intermediate and large diameters (Fig. 5). As expected the diameter and height ranges for silver fir were greater than for the beech.

The CWD volume was 420 m^3ha^{-1} (Tab. 2) representing 40.8% of the volume of living trees. The volume of logs (71.4%), within the total volume of CWD, was much greater than the volume of snags/standing dead trees and stumps. As far as the CWD profile is concerned (Tab. 3), all the decay classes were represented, but decay class 4 was the modal value (38,3% of the total CWD) and it was followed by classes 3, 2, 5 and class 1 which represents the recent dead trees and which had a lower volume than the others. In the different CWD types, decay class 4 was the modal value for stumps (87.3%) and logs (41.7%), but not for snags where the modal class was the third (24.8%).

The absence of bark and the decay rate made the identification of the species problematic for most of the samples in classes 3, 4 and 5 (more than 80% of the samples). The logs were mainly found in the small-intermediate tree size (diameter < 70 cm) while the snags were dominant in the large diameter size (> 70 cm) (Fig. 6).

The large living trees in the studied area were among the largest and highest observed in this region (Holeksa et al. 2009), reaching 163 cm of dbh and 58 m height for silver fir and 152 cm dbh and 62 m height for Norway spruce. The maximum tree age observed in the recent natural stumps was more than 400 years for silver fir and Norway spruce and more than 300 years for beech.

Discussion

The Biogradska Gora mixed *Abies-Picea-Fagus* forest is one of the largest old-growth forest remaining (1230 ha) in central-southern Europe. It shows the typical structural characteristics of old-growth forests: large (> 150 cm dbh) and old trees (>400 y), relevant volumes of living tree (1029.6 m^3ha^{-1}) and of coarse woody debris (420.6 m^3ha^{-1}) in different decay classes and with horizontal and vertical structural complexity (Franklin & Spies 1991). The volumes of living trees and of CWD are among the highest observed so far in central-southern Europe (Tab. 4). The studied area is very structurally complex but relatively uniform in terms of internal variability as can be seen from the relatively small range and SD of each analyzed parameter (Tabs. 1, 2). According to the number of individuals, beech is the dominant species but, from the volume point of view, the most represented species is silver fir. Norway spruce is scarce from the regeneration to the small and intermediate diameters while it is the second species represented in the dominant layer in terms of volume and of number of individuals. The other species (mainly sycamore maple, mountain ash and wych elm) only occur in the regeneration (where they are relatively abundant) and in the small and intermediate trees diameter classes but are absent in the dominant layers (large trees). This kind of irregular species distribution has been observed in other old-growth forests of the same type thus showing a common development pattern (Mikac et al. 2013; Motta et al. 2011; Nagel & Svoboda 2008). Compared to silver fir and Norway spruce, beech and the other broadleaves are more competitive in a higher light environment, due to their faster height growth (Burschel & Mosandl 1985; Rozenbergar et al. 2007). On the other hand, if too much time is spent in the shade, beech and the other broadleaves may lose their ability to produce an upright stem (Diaci & Kozjek 2005) and the beech crown becomes plagiotropic, or flat (Rozenbergar et al. 2007), while other broadleaves develop an umbrella-like crown (Petrițan et al. 2009). In a disturbance regime characterized by small-scale disturbances, where there is not enough light for new regeneration establishment and the gap fillers are mainly previously suppressed trees, it is much more difficult for beech and other broadleaves to compete with silver fir and spruce. In fact silver fir and Norway spruce have a high capacity to tolerate shading and suppression, and can show a vigorous growth response after release (Ferlin 2002) thus making beech under-represented in the dominant layers (Schütz 1992; 2001). The persistence of less shade tolerant species such as maple, ash and elm, is linked to disturbances that create canopy openings > 400 m^2 (Nagel et al. 2010). A good indicator of former medium-large gaps in the studied site was the presence of small maple sycamore stands, which were observed between the plots and just outside the studied area. Maple is a more light demanding species, compared to fir, beech or Norway spruce, and can access the canopy through its rapid early growth in relatively large canopy gaps (Petritan et al. 2007). These small patches of mono-layered maple stands have highlighted a different development process than the most represented mixed and multilayered matrix. The same feature was observed in the same region in Lom (Motta et al. 2011) and in Perućica (Nagel et al. 2014)

When the analysis was upscaled and the whole forest was observed through satellite images no important differences were observed. The medium-large canopy gap ratio (gaps > 150 m^2) was very low (< 0,2%) since only 18 forest canopy gaps were detected in 1230 ha of *Abies-Picea-Fagus* forest. Since in previous studies the observed total canopy gap ratio (gaps > 10 m^2) was between 15 and 20% for the same forest type (Bottero et al. 2011; Nagel & Svoboda 2008), only a very small part of the canopy opening can be considered to be due to medium-large canopy gaps and most of the canopy disturbances could be related to very small-scale events (10-150 m^2) caused by both autogenic and allogenic disturbances. Considering the size of the old-growth of Biogradska Gora it was here assumed that it was possible to capture the full range of the structural spatio-temporal variability (Cissel et al. 1999; Fraver et al. 2009; Landres et al. 1999). In the Biogradska Gora forest it was not possible to exclude *a priori* that larger intermediate or stand replacing disturbances occurred in the past (having a return time longer than the one studied) and that they are part of the current disturbance regime. However if these events occur, they are rare and would only temporarily modify the species composition and the structure in the context of the long-term history of small scale gap dynamics (Romme et al. 1998; Sprugel 1991). The fact that some long-term research has shown that the total volume of living trees over long periods is relatively stable despite the occurrence of both small and intermediate disturbances in Dinaric beech-fir old-growth forests (Diaci et al. 2011) and in a mixed beech-fir-Norway spruce forest (Motta et al. 2011) would seem to support this hypotheses.On the bases of the previous evidence, it is possible to state that the forest dynamics in Biogradska Gora are dominated by very small-scale processes, partially autogenic and partially allogenic. The influence of large scale or intermediate disturbances are negligible. In other forest types within the same region it has been observed that the disturbance regime can vary from large stand-replacing disturbances e.g. severe windstorms followed by insect outbreaks in montane and subalpine Norway spruce forests (Svoboda et al. 2013) to intermediate disturbances e.g. windstorms in montane beech, silver fir forests (Nagel & Diaci 2006) and to small-scale autogenic processes with scattered intermediate wind disturbances (Motta et al. 2011). The Biogradska Gora forest can be placed at the far end of a gradient that ranges from forests controlled by stand-replacing disturbances to those where very small-scale processes dominate. This phase of the development, which is the typical old-growth stage, can last for a relatively long period of time (evidence exists of for some centuries, but it could be even longer) even though the authors are well aware of the fact than when different spatial and temporal scales are used the observed process could be more complex (Turner et al. 1993). In fact over the last decade, the accumulation of evidence has shown that disturbances are key processes in forest ecosystem dynamics but, during the same period, in some regions and for some forest types e.g. mixed forests in the montane belt of the Biogradska Gora old-growth forest, a relatively stable structure can persist for relatively long periods (Motta et al. 2011; Parish & Antos 2004; 2006).

Acknowledgements

Spot Image Inc. are gratefully acknowledged for having provided the satellite imagery and image processing systems (Planet Action project: Bosnian old-growth forests). We are grateful to the Biogradska Gora National park administration for providing access to the Forest Reserve. We would like to thank the two anonymous reviewers for their useful suggestions concerning an earlier version of the manuscript and Marguerite Jones for the final language editing.

References

Alessandrini A, Biondi F, Di Filippo A, Ziaco E, Piovesan G. 2011. Tree size distribution at increasing spatial scales converges to the rotated sigmoid curve in two old-growth beech stands of the Italian Apennines. For Ecol Manage 262: 1950-62.

Andjelić M, Dees M, Pantić D, Borota D, Šljukić B, Čurović M. 2012. Status of forest resources of Montenegro. Agriculture & Forestry 57: 39-52.

Anić I, Mikac S. 2008. Structure, texture and regeneration of dinaric beech-fir virgin forest of Čorkova uvala. Šumarski List 132: 505-15.

Barbati A, Salvati R, Ferrari B, Di Santo D, Quatrini A, Portoghesi L, Travaglini D, Iovino F, Nocentini S. 2012. Assessing and promoting old-growthness of forest stands: Lessons from research in Italy. Plant biosyst 146: 167-74.

Bilovitz PO, KnežEvić B, StešEvić D, Mayrhofer H. 2009. Lichenized and lichenicolous fungi from Bjelasica (Montenegro) with special emphasis on the Biogradska Gora National Park. Bibliotheca Lichenologica 99: 67-80.

Bottero A, Garbarino M, Dukić V, Govedar Z, Lingua E, Nagel TA, Motta R. 2011. Gap-phase dynamics in the old growth forest of Lom (Bosnia-Herzegovina). Silva Fennica 45: 865-73.

Bruyninx C, Habrich H, Söhne W, Kenyeres A, Stangl G, Völksen C. 2012. Enhancement of the EUREF Permanent Network Services and Products. In Geodesy for Planet Earth, eds Kenyon, S, Pacino, MC and Marti, U, 27-34: Springer Berlin Heidelberg.

Burrascano S, Keeton WS, Sabatini FM, Blasi C. 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. For Ecol Manage 291: 458-79.

Burschel P, Mosandl R. 1985. Waldbau angesichts neuartiger Wladschäden. In Die Sache Mit dem Wald, 269-80.

Cissel JH, Swanson F, Weisberg PJ. 1999. Landscape management using historical reference fire regimes: Blue River, Oregon. Ecol Appl 9: 1217-31.

Clements FE. 1936. Nature and Structure of the Climax. J Ecol 24: 252-84.

Čurović M. 2011. Forest types in National Park Biogradska Gora (Dissertation) Available from: Faculty of Forestry, University of Belgrade.

Čurović M, Medarević M, Cvjetićanin R, Knežević M. 2011a. Major characteristics of mixed fir and beech virgin forests in the National park Biogradska gora in Montenegro. Bulletin of the Faculty of Forestry 103: 157-72.

Čurović M, Medarević M, Pantić D, Spalević V. 2011b. Major types of mixed forests of spruce, fir and beech in Montenegro. Centralb gesamte Forstwes 128: 93-111.

Diaci J ed. 1999. Virgin Forests and Forest Reserves in Central and East European Countries. Ljubljana.

Diaci J, Kozjek L. 2005. Beech sapling archiecture following small and medium gap disturbances in silver fir-beech old-growth forests in Slovenia. Schweiz Z Forstwes 156: 481-86.

Diaci J, Rozenbergar D, Anic I, Mikac S, Saniga M, Kucbel S, Visnjic C, Ballian D. 2011. Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. Forestry 84: 479-91.

Diaci J, Rozenbergar D, Boncina A. 2010. Stand dynamics of Dinaric old-growth forest in Slovenia: Are indirect human influences relevant? Plant biosyst 144: 194-201.

Farrell EP, Führer E, Ryan D, Andersson F, Hüttl R, Piussi P. 2000. European forest ecosystems: building the future on the legacy of the past. For Ecol Manage 132: 5-20.

Ferlin F. 2002. The growth potential of understorey silver fir and Norway spruce for uneven-aged forest management in Slovenia. Forestry 75: 375-83.

Foster DR, Orwig DA, Mclachlan JS. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. Trends Ecol Evol 11: 419-24.

Franklin J, Spies TA, Pelt RV, Carey AB, Thornburgh DA, Berg DR, Lindenmayer DB, Harmon ME, Keeton WS, Shaw DC, Bible K, Chen J. 2002. Disturbance and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fire forests as an example. For Ecol Manage 155: 399-423.

Franklin JF. 1993. Lesson from old-growth. J For 91: 10-13.

Franklin JF, Spies TA. 1991. Ecological definitions of old-growth Douglas-fir forests. In Wildlife and vegetation of unmanaged Douglas-fir forests, eds Ruggiero, LF, Aubry, KB, Carey, AB and Huff, MH, 61-69. Portland: USDA Forest Service, Pacific Northwest Research Station.

Franklin JF, Van Pelt R. 2004. Spatial Aspects of Structural Complexity in Old-Growth Forests. J For 102: 22-28.

Fraver S, White AS, Seymour RS. 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. J Ecol 97: 289-98.

Garbarino M, Borgogno Mondino E, Lingua E, Nagel T, Dukić V, Govedar Z, Motta R. 2012. Gap disturbances and regeneration patterns in a Bosnian old-growth forest: a multispectral remote sensing and ground-based approach. Ann For Sci 69: 617-25.

Garbarino M, Lingua E, Weisberg P, Bottero A, Meloni F, Motta R. 2013. Land-use history and topographic gradients as driving factors of subalpine *Larix decidua* forests. Landsc Ecol 28: 805-17.

Garbarino M, Weisberg PJ, Motta R. 2009. Interacting effects of physical environment and anthropogenic disturbances on the structure of European larch (*Larix decidua* Mill.) forests. For Ecol Manage 257: 1794-802.

Gascon C, Williamson GB, Da Fonseca GaB. 2000. Receding Forest Edges and Vanishing Reserves. Science 288: 1356-58.

Gimmi U, Bürgi M, Stuber M. 2008. Reconstructing anthropogenic disturbance regimes in forest ecosystems: a case study from the Swiss Rhone Valley. Ecosystems 11: 113-24.

Holeksa J, Saniga M, Szwagrzyk J, Czerniak M, Staszynska K, Kapusta P. 2009. A giant tree stand in the West Carpathians-An exception or a relic of formerly widespread mountain European forests? For Ecol Manage 257: 1577-85.

Janowiak MK, Nagel LM, Webster CR. 2008. Spatial Scale and Stand Structure in Northern Hardwood Forests: Implications for Quantifying Diameter Distributions. For Sci 54: 497-506.

Král K, Vrška T, Hort L, Adam D, Šamonil P. 2010. Developmental phases in a temperate natural spruce-fir-beech forest: determination by a supervised classification method. Eur J For Res 129: 339-51.

Landres PB, Morgan P, Swanson FJ. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol Appls 9: 1179-88.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E. 2002. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Cons Biol 16: 605-18.

Marchetti M, Tognetti R, Lombardi F, Chiavetta U, Palumbo G, Sellitto M, Colombo C, Iovieno P, Alfani A, Baldantoni D, Barbati A, Ferrari B, Bonacquisti S, Capotorti G, Copiz R, Blasi C. 2010. Ecological portrayal of old-growth forests and persistent woodlands in the Cilento and Vallo di Diano National Park (southern Italy). Plant biosyst 144: 130-47.

Maunaga Z. 2001. Management plan for forests with special purpose in the strict natural reservations "Janj" and "Lom". Banja Luka: Bosnia and Herzegovina Forestry project. Republic of Srpska.

Mikac S, Klopf M, Anić I, Hasenauer H. 2013. Using the tree growth model MOSES to assess the dynamics of Dinaric old-growth mixed beech–fir forest ecosystems. Plant biosyst 147: 664-71.

Motta R. 2002. Old-growth forests and silviculture in the Italian Alps: the case-study of the strict reserve of Paneveggio (TN). Plant biosyst 136: 223-32.

Motta R, Berretti R, Castagneri D, Dukić V, Garbarino M, Govedar Z, Lingua E, Maunaga Z, Meloni F. 2011. Toward a definition of the range of variability of central European mixed *Fagus-Abies-Picea* forests: the nearly steady-state forest of Lom (Bosnia and Herzegovina). Can J For Res 41: 1871-84.

Motta R, Berretti R, Castagneri D, Lingua E, Nola P, Vacchiano G. 2010. Stand and coarse woody debris dynamics in subalpine Norway spruce forests withdrawn from regular management. Ann For Sci 67: 803p1_03p8.

Motta R, Berretti R, Lingua E, Piussi P. 2006. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. For Ecol Manage 235: 155-63.

Nagel TA, Svoboda M, Rugani T, Diaci J. 2010. Gap regeneration and replacement patterns in an old-growth Fagus–Abies forest of Bosnia–Herzegovina. Plant Ecol 208: 307-18.

Nagel TA, Diaci J. 2006. Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. Can J For Res 36: 629-38.

Nagel TA, Svoboda M. 2008. Gap disturbance regime in an old-growth *Fagus-Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. Can J For Res 38: 2728-37.

Nagel TA, Svoboda M, Kobal M. 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecol Appl. DOI: 10.1890/13-0632.1

Oliver CD, Larson BC. 1996. Forest Stand Dynamics. New York: John Wiley & Sons.

Parish R, Antos JA. 2004. Structure and dynamics of an ancient montane forest in coastal British Columbia. Oecologia 141: 562-76.

Parish R, Antos JA. 2006. Slow growth, long-lived trees, and minimal disturbance characterize the dynamics of an ancient montane forest in coastal British Columbia. Can J For Res 36: 2826-38.

Peterken GF. 1996. Natural woodland. Ecology and conservation in northern temperate regions. Cambridge: Cambridge University Press.

Petriţan A, Lüpke B, Petriţan I. 2009. Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings. Eur J For Res 128: 61-74.

Petritan AM, Von Lüpke B, Petritan IC. 2007. Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. Forestry 80: 397-412.
Romme WH, Everham EH, Frelich LE, Moritz MA, Sparks RE. 1998. Are Large, Infrequent Disturbances Qualitatively Different from Small, Frequent Disturbances? Ecosystems 1: 524-34.
Rozenbergar D, Mikac S, Anic I, Diaci J. 2007. Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech fir forest reserves in South East Europe. Forestry 80: 431-43.
Runkle JR. 1982. Patterns of disturbance in some old-growth mesic forest of eastern North-America. Ecology 63: 1533-46.
Schuck A, Hytönen T. 2000. Forest Reserve Research Network. In *COST Action E4*, 195.
Schütz JP. 1992. Die waldbaulichen Formen und die Grenzen der Plenterung mit Laubbaumarten. Schweiz Z Forstwes 143: 442-60.
Schütz JP. 2001. Opportunities and strategies of transforming regular forests to irregular forests. For Ecol Manage 151: 87-94.
Sprugel DG. 1991. Disturbance, equilibrium, and environmental variability: What is "Natural' vegetation in a changing environment? Biol Cons 58: 1-18.
Svoboda M, Janda P, Bače R, Fraver S, Nagel TA, Rejzek J, Mikoláš M, Douda J, Boublík K, Šamonil P, Čada V, Trotsiuk V, Teodosiu M, Bouriaud O, Biriş AI, Sýkora O, Uzel P, Zelenka J, Sedlák V, Lehejček J. 2013. Landscape-level variability in historical disturbance in primary Picea abies mountain forests of the Eastern Carpathians, Romania. J Veg Sci: DOI: 0.1111/jvs.12109
Turner MG, Romme WH, Gardner RH, O'neill RV, Kratz TK. 1993. A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes. Landsc Ecol 8: 213-27.
Van Wagner CE. 1968. The line intersect method in forest fuel sampling. For Sci 14: 20-26.
Ziaco E, Di Filippo A, Alessandrini A, Baliva M, D'andrea E, Piovesan G. 2012. Old-growth attributes in a network of Apennines (Italy) beech forests: Disentangling the role of past human interferences and biogeoclimate. Plant biosyst 146: 153-66.

Table 1. Structural characteristics (density, basal area, volume of living trees and density of regeneration) in the mixed silver fir, beech and Norway spruce Biogradska Gora old-growth forest

	Density [n ha^{-1}]	Basal area [m^2 ha^{-1}]	Volume [m^3 ha^{-1}]	Regeneration [n ha^{-1}]
Silver fir	92 (22.3%)	34.1 (56.7%)	630.6 (61.2%)	299 (9.6%)
Beech	298 (72.3%)	18.7 (18.7%)	262.6 (25.5%)	1903 (61.2%)
Norway spruce	10 (2.4%)	5.6 (9.3%)	112.4 (10.9%)	46 (1.5%)
Sycamore maples	10 (2.4%)	1.5 (1.5%)	23.7 (2.3%)	511 (16.4%)
Other species	2 (0.5%)	0.1 (0.1%)	0.6 (0.1%)	348 (11.2%)
Total	412	60.1	1029.6	3107
Range	265-663	26.5-103.1	352.8-1232.9	276-12640
St. dev.	119	11.0	486.8	3444

	Snag [m^3 ha^{-1}]	Log [m^3 ha^{-1}]	Stump [m^3 ha^{-1}]	Total [m^3 ha^{-1}]
Volume	114.2	300.0	6.2	420.4
Range	0-403.6	2.2-604.3	0-25.2	68.9-736.5
St. dev.	125.1	152.0	7.4	193.4

Table 2. CWD volume (snags, logs and stumps) in the mixed silver fir, beech and Norway spruce Biogradska Gora old-growth forest

	Class 1	Class 2	Class 3	Class 4	Class 5
Stumps	0,1	3,9	9,1	87,3	0,0
Logs	2,8	9,0	34,3	41,7	12,3
Snags	8,1	22,3	42,8	26,8	0,0
Total	4,2	12,5	36,2	38,3	8,8

Table 3. % of CWD (stumps, logs, snags and total) in different decay classes.

	Country	Altitude [m s.l.m.]	Species*	Density [n ha^{-1}]	Basal area [m^{2}ha^{-1}]	Volume [m^{3}ha^{-1}]	CWD	Reference
Biogradska gora	Montenegro	1210-1450	Fs, Aa, Pa, Ap	412	60.1	1029.6	420.4	This paper
Perućica	Bosnia-Herzegovina	1420-1520	Aa, Pa, Fs	432	59.1	1031.1	406.0	2012, unpublished data
Lom	Bosnia-Herzegovina	1250-1522	Fs, Aa, Pa	489	47.1	763.1	327.3	Motta et al., 2011
Labowiec Reserve	Poland	840-960	Fs, Aa	n.a.	36.3	543.0	383.0	Paluch, 2007
Suchy Zleb	Poland	1070-1120	Fs, Aa, Pa	442	36.7	446.8	159.0	Szwagrzyk et al., 2006
Čorkova uvala	Croatia	850-1000	Aa, Fs, Pa	440	42.7	671.2	n.a.	Anic, Mikac, 2008
Hrončkovský grúń	Slovakia	730-1050	Fs, Pa, Fe, Ap, Aa	243	41.8	724.4	306.0	Holeksa, 2009
Plješevica	Bosnia-Herzegovina	1120	Fs, Aa, Pa,Ap, Fe	n.a.	n.a.	651.5	89.0	Visnjic et al. 2009

Table 4. Stand characteristics for some mixed silver fir, beech and Norway spruce in southern-central European old-growth forests.

Figure captions

Fig. 1. Location of the Biogradska Gora National park.

Fig. 2. Map of the Biogradska Gora valley showing the main vegetation types and the location of the 30 plots.

Fig. 3. Diameter class distribution in the mixed silver fir, beech, Norway spruce old-growth forest of Biogradska Gora. The distribution shows a rotated sigmoidal form ($P < 0.05$) which is typical of old-growth stands.

Fig. 4. Relative abundance of the most abundant tree species according to the size class (from regeneration to dominant trees) showing stratification of the species.

Fig. 5. Diameter-height relationships in beech and silver fir. The diameters are measured at the breast height (dbh).

Fig. 6. Log and snag size distribution.

Fig. 1. Location of the Biogradska Gora National park.
209x127mm (72 x 72 DPI)

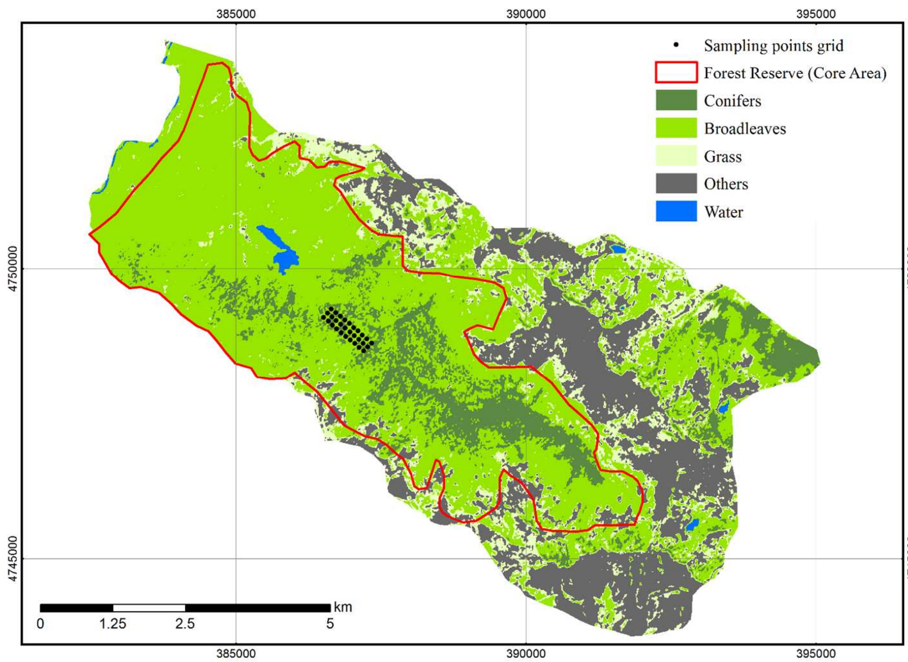


Fig. 2. Map of the Biogradska Gora valley showing the main vegetation types and the location of the 30 plots
148x105mm (300 x 300 DPI)

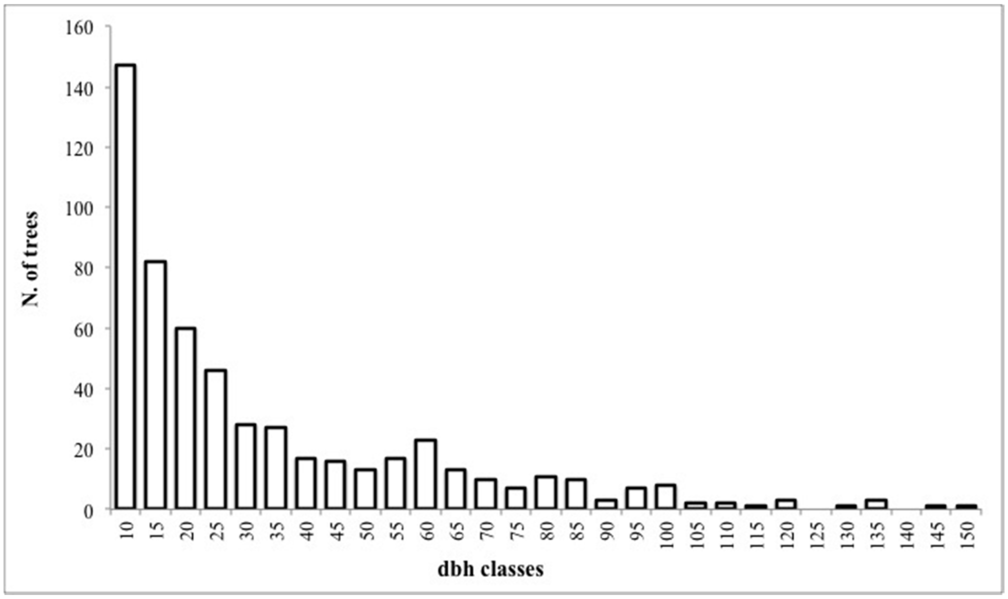


Fig. 3. Diameter class distribution in the mixed silver fir, beech, Norway spruce old-growth forest of Biogradska Gora. The distribution shows a rotated sigmoidal form (P < 0.05) which is typical of old-growth stands.
252x149mm (72 x 72 DPI)